

APOMIXIS AS RELATED TO GEOGRAPHICAL DISTRIBUTION IN THE PANICOID GRASS TRIBES*

By WALTER V. BROWN

(*The Grass Research Project, Plant Research Institute, University of Texas*)

A number of South African botanists and plant breeders have asked me why apomixis is so common among grasses of South Africa as indicated by Brown and Emery (1957). From the large number of apomictic species reported (25) in the relatively small number of species examined (50), it would seem to be true that apomixis is unusually common among grasses of that region.

In a subsequent paper, Brown and Emery (1958) have demonstrated that apomixis is apparently far more common in genera of the subfamily Panicoideae than in any other comparable group of the family (Table I). In the subfamily Festucoideae apomixis by agamospermy is evidently sporadic and is known to occur in only three genera in three different tribes. In contrast, apomixis appears to be a characteristic feature of the Panicoideae, occurring in many genera of the tribes Paniceae, Andropogoneae, Chlorideae, Eragrosteae, and Pappophoreae. Because of the apparent uniformity of mechanism (4-nucleate unreduced embryo sacs) and high frequency of apomictic species, Brown and Emery (1958) proposed the hypothesis that the same genes for apomixis are widely distributed among sexual as well as apomictic genera of these tribes and have been so since the origins of these tribes perhaps 100,000,000 years ago.

Almost without exception apomictic grasses are polyploid and perennial although many polyploid and perennial species are sexual. It was proposed, however, that many of the sexual (diploid, polyploid, perennial, and annual) species of the Panicoideae probably contain one or a few of the many genes necessary for an effective, balanced apomictic system. Such species would be sexual since they would lack most of the

* Too late for inclusion in this publication is knowledge of the paper by Jacques de Coulon, 1923; *Nardus stricta*; Etude physiologique, anatomique et embryologique; Mem. Soc. vaudoise des Sci. Nat. No. 6: 247-332. He demonstrated complete failure of pollination by abortion of stamens but normal seed production in some strains. Normal anthesis but inability to germinate pollen, no observable pollen tubes entering the embryo sac, and persistence of both synergids indicated apomixis in other strains. This is the first known report of apomixis in grasses. Since the embryo sac is a normal 8-nucleate type derived from a vacuolate megaspore mother cell and no evident aposporous embryo sacs, the process is diplospory without pseudogamy followed by parthenogenesis.

necessary genes for apomixis but they would, nevertheless, serve as carriers of one or more apomictic genes.

TABLE I
APOMICTIC GRASSES

Viviparous

Agrostis			
stolonifera	V	Circum north polar	(13, 22)
tenuis	V	N. Europe	(13, 22)
Deschampsia			
alpina	V	N. Europe	(13, 22)
caespitosa	V	Circum north polar	(13, 22)
rhenana	V	N. Europe	(13, 22)
Festuca			
ovina	V	Circum north polar	(13, 22)
rubra	V	Circum north polar	(13, 22)
Poa			
bulbosa	V	Europe	(13, 22)
arachnifera	V	U.S.A.	(22)
jemtlandica	V	Europe	(13, 22)
arctica	V	Arctic	(13, 22)

Agamospermous

A = Aposporous

D = Diplosporous

FESTUCOIDEAE

FESTUCEAE

Poa			
alpina	D	arctic	(13, 22)
ampla	A	U.S.A.	(22)
arctica	A	arctic	(13, 22)
arida	A	U.S.A.	(22)
compressa	A	Europe	(13, 22)
glaucæ	D	U.S.A.	(22)
nemoralis	D	U.S.A.	(13, 22)
nervosa	D	U.S.A.	(12, 22)
palustris	D	Circum north polar	(13, 22)
pratensis	A	N. temperate	(13, 22)

AGROSTIDEAE

Calamagrostis			
canadensis	D	N. Amer.	(21, 22)
chalybaea	D	N. Europe	(20, 22)
inexpansa	D	N. Amer.	(21, 22)
langsdoiffii	D	N. Asia	(21, 22)
lapponica	D	Europe	(20, 22)
purpurascens	D	N. Europe	(21, 22)
purpurea	D	N. Europe	(20, 22)

HORDEAE			
Agropyron			
scabrum	D	New Zealand	(14)
PANICOIDEAE			
(EUPANICOIDEAE)			
ANDROPOGONEAE			
Bothriochloa			
decipiens	A	Australia	(4)
ewartiana	A	Australia	(4)
intermedia	A	Africa to Australia	(2, 4, 7)
= caucasica?		Caucasus	(7)
= glabra?		S. Asia	(4, 7)
ischaemum	A	Europe to Formosa	(3, 4, 7)
pertusa	A	E. Africa, S. Asia	(2, 4, 7)
= inculpta?		E. Africa, S. Asia	(7)
radicans	A	Africa	(2, 4)
venusta	A	Ceylon	(4, 7)
Capillipedium			
parviflorum	A	Africa to Australia	(4, 7)
spicigerum	?		(7)
Dichanthium			
annulatum	A	N. Africa, China, Aust.	(2, 4, 7)
caricosum	A	S. Asia	(2, 4, 7)
nodosum	A	India	(4)
Heteropogon			
contortus	A	Mex., U.S., Africa	(2, 4, 9)
		Aust., India, Java	
Hyparrhenia			
hirta	A	Africa, S. Asia	(2, 4)
rufa	A	South Africa	(2, 4)
Saccharum			
officinarum	Not proved apomictic;	S. E. Asia	
spontaneum	Price, S. Unpublished.	S. E. Asia	
Themeda			
quadrivalvis	A	India	(4)
triandra	A	South Africa	(2, 3, 4)
MAYDEAE			
Tripsacum			
dactyloides	D	U.S.A.	(4, 10)
PANICEAE			
Anthephora			
pubescens	A	South Africa	(2, 4)
Brachiaria			
brizantha	A	South Africa	(2, 4)
serrata	A	South Africa	(2, 4)

Cenchrus			
setigerus	A	India	(11)
Echinochloa			
frumentacea	Occasional A	India	(25)
Eriochloa			
borumensis	A	South Africa	(2, 4)
sericea	A	U.S.A.	(4)
Panicum			
deustum	A	South Africa	(2, 4)
maximum	A	Africa	(4, 26)
obtusum	A	U.S.A.	(4)
virgatum	A	U.S.A.	(4)
Paspalum			
dilatatum	A	South America	(4, 16)
hartwegianum	A	Texas, Mexico	(4)
malacophyllum	A	South America	(4)
notatum	A	South America	(6)
scrobiculatum	Occasional A	India	(26)
secans	A	America	(23)
Pennisetum			
ciliare	A	Asia, Africa	(11, 24)
clandestinum	A	Asia, Africa	(17)
orientale	A	Asia	(17)
purpureum	A	Asia, Africa	(2, 4)
ramosum	Occasional A	Asia, Africa	(17)
setaceum	A	Asia, Africa	(17)
villosum	A	Asia, Africa	(17)
Setaria			
leucopila	A	U.S.A.	(8)
villosissima	A	U.S.A.	(8)
Tricholaena			
monachne	A	South Africa	(2, 4)
Urochloa			
bolbodes	A	South Africa	(2, 4)
mosambicensis	A	South Africa	(2, 4)
pullulans	A	South Africa	(2, 4)
trichopus	A	South Africa	(2, 4)

PANICOIDEAE

(CHLORIDOIDEAE)

CHLORIDEAE

Chloris			
gayana (4n)	A	Africa	(2, 4)
Bouteloua			
curtipendula	A	U.S.A.	(4, 5)
Buchloë			
dactyloides	Occasional A	U.S.A.	(4)
Fingerhuthia			
africana	D	South Africa	(2, 4)

ERAGROSTEAE

Eragrostis			
chloromelas	D?	South Africa	(2, 4)
curvula	D?	South Africa	(2, 4)
heteromera	D?	South Africa	(2, 4)

PAPPOPHOREAE

Schmidtia			
bulbosa	?	South Africa	(2, 4)
kalahariensis	?	South Africa	(2, 4)

Hybridizations among such carrier species would occasionally bring together in polyploid hybrids all necessary genes for effective apomictic systems. Because apomixis is essentially restricted to polyploid forms, it has been assumed that polyploidy provides a genetic environment in which apomixis is best able to be expressed (Stebbins, 1950).

The sexual parental forms together with the hybrid apomictic "micro-species" constitute an agamic complex within the genus. Although the sexual ancestral forms may be typical species and treated as such taxonomically, the apomictic derivatives form a polymorphic complex within which species in the usual sense do not exist (Stebbins, 1950).

If the above hypothesis is correct, if apomixis in the Panicoideae is more than just the sporadic development of agamic complexes, a large number of apomictic species would be expected in these tribes (Table 1). Even the percentage of apomictic species should be high, as high as 25 to 30 per cent of all species as reported by Brown and Emery (1958). Evolution within these tribes is characterised, therefore, not only by polyploidy but also by apomixis, the two being intimately related and producing many agamic complexes. Apomixis, like polyploidy, is a major factor in the species problem and is a dominating feature of taxonomic considerations of apomixis-containing genera.

Apomictic Panicoideae, abundant in South Africa, are not lacking, however, in the New World: *P. dilatatum* and *P. notatum* (Burton, 1948); *Bouteloua curtipendula* (Bryant, 1952); *Tripsacum dactyloides* (Farquharson, 1955); *Setaria leucopila* and *S. villosissima* (Emery, 1957); *Paspalum secans* (Snyder, 1957); *Eriochloa sericea*, *Panicum obtusum*, *P. virgatum*, *Paspalum hartwegianum*, *P. malacophyllum*, and *Heteropogon contortus* (Brown and Emery, 1958). There are 13 New World apomictic Panicoideae now known, but 30 have been reported from the Old World (Brown and Emery, 1957; Narayan, 1951; Snyder *et al.*, 1955; Warmke, 1954). From present information it appears that apomictic species are more common among Old World than among the New World panicoid

grasses. But whether this present knowledge reflects a true picture or a distorted one is not now known because of too limited data. The New World species examined constitute a truer representative sample of the whole population than the Old World species since the latter were selected by the unknown original seed collectors as possible forage grasses for introduction in the United States. They are, therefore, mostly polyploid and perennial, and selection for desirable forage types may have constituted unintentional selection for apomixis.

Among the Andropogoneae the evidence strongly indicates a greater concentration of apomictic species in the Old World. The only known native apomictic species of Andropogoneae in the New World is *Heteropogon contortus*, a species also native in the Old World. If our present knowledge of the geographical distribution of apomixis in the Andropogoneae represents a reasonably true picture, it is possible to correlate apomixis with the length of time representatives of Andropogoneae have occupied the various continental areas. Hartley states (1950) that, "Sub-normal values (of species in the grass flora) are particularly common in the tropical parts of the American continent, suggesting that the tribe may not yet have attained its maximum development in the western hemisphere. This supposition is supported by the fact that the localities in which the percentage of species of Andropogoneae in the grass flora is more than twice the normal figure are grouped together in the south-east Asia region. The Andropogoneae are generally recognised as the most advanced of the major grass tribes and the data suggest that they have spread outward from a centre of distribution in south-east Asia and have not yet attained full development in distant regions." His Fig. 3 indicates that the Andropogoneae are represented in the African grass flora in an above-normal percentage. It is possible, therefore, that apomictic species are more abundant toward the centre of distribution of the tribe, that is, in Southern Asia and also in Africa, but less abundant in distant regions, the Americas.

As species of a genus or tribe spread outward from a centre of origin the sexual species, and especially diploid species (Gustafsson 1946-47), as a result of their variability, should be able to occupy a variety of new habitats and therefore migrate rapidly. Obligate apomictic taxa, on the other hand, would have very little variability. Facultative apomicts have some variability but less than sexual species. Apomictic taxa would be left behind in the original habitats for which they were adapted and to which they had become restricted. Sexual types that might or might not be carriers of apomictic genes would constitute the majority of taxa at the periphery of the occupied area and would give rise to the new species in the more recently occupied regions. It may be that the rela-

tively few American species of Andropogoneae represent rather recently arrived taxa that have not had time to produce many agamic complexes although genes for apomixis may be present in the gene pools of some of the genera.

On the other hand, providing constancy of environments, the apomicts in the original Old World areas might have been extremely well adapted and have accumulated in great number of species and individuals. The sexual diploid progenitors may now have been eliminated by the apomicts, may be restricted to small areas, or may be common within the ranges of the apomicts.

In the Paniceae, on the other hand, there are known to be 12 apomictic species in the western hemisphere and about 17 in the eastern, an approximately even distribution around the world (Table 1). Hartley (1950) reported species of Paniceae in above normal percentages in the hot moist regions of both hemispheres, "having originated probably in eastern tropical America and having spread widely through the moist tropical regions of the world". If large numbers of apomictic species are correlated with extremely long occupancy of a region, it is likely that the tribe Paniceae is a very old group that has been well established in both hemispheres for a very long time.

Although apomixis has been reported in three tribes of the Chloridoideae (Chlorideae, Eragrosteae, and Pappophoreae), too few species have been studied for generalisations to be made. All but one of the presently known apomicts in these tribes are South African. Hartley concluded for the Eragrosteae that, "There is thus no indication that the tribe has failed to achieve its full potential expansion in most parts of the world", being especially, "abundant in regions of high winter temperature and low rainfall". It is likely that the same conclusion would apply equally well to the Chlorideae and Pappophoreae.

The above hypothesis that relates apomixis with the centre of origin of an expanding tribe is not supported by evidence from the genus *Crepis* (Babcock, 1947). The centre of origin of that genus, in fact of the whole subtribe Crepidinae, is Central Asia, but the only known apomictic species of *Crepis* are native in Western United States, apparently on the periphery of the range of the genus. Stebbins and Babcock (1939) stated, however, that diploid species of *Crepis* reached America and then acquired polyploidy and apomixis more or less simultaneously. *Crepis* is, essentially, a diploid genus with essentially no polyploidy among the species of the most primitive sections in Asia. Lack of apomixis among the primitive species may be correlated with lack of polyploidy, or, on the other hand, apomixis may have arisen spontaneously by mutations and hybridisa-

tions in America. There may not be genes for apomixis in the gene pool of the genus as a whole, although two other genera of the subtribe Crepidineae contain apomictic species, *Taraxacum* and *Hieracium*. The sexual and apomictic species of *Taraxacum* occur naturally in Eurasia, essentially the region of origin. The apomictic species of *Hieracium* are found in the area of origin of the tribe with only sexual species (as far as known) in distant regions. It is possible, therefore, that the distribution of sexual and apomictic species of the subtribe Crepidineae of the Compositae supports the hypothesis proposed here for tribes of the Gramineae.

Apomixis is known to occur in many other plant families and genera. Too little is known about the methods of reproduction in most species of such families and the relationships of reproductive methods to geographical distribution are not well enough known to warrant the use of such information as a test of the hypothesis at this time. It is quite likely, however, that certain tribes of the Compositae may have apomictic genes widely distributed among their genera as seems to be true of tribes of Panicoideae of the Gramineae.

South Africa, then, is a region favoured by many apomictic grasses. It lies within or close to the original area of the Andropogoneae, the Paniceae have been present in its flora long enough for apomixis to have become well established, and the Chloridoideae have found suitable habitats in its drier regions. It is quite likely that the grass flora of Southern Asia is characterized by a high percentage of apomictic species for the same reasons.

The hypothesis presented here is tentative and needs a great deal of testing. At present only a very small fraction of the thousands of species of Panicoideae have been examined or tested for apomixis. There is little doubt but that many more species will be found to be apomictic but it will be a long time before any relationships between apomixis, age, and geographical area will be known for certain. In the meantime, a large number of known and unknown agamic complexes need to be studied in detail to determine: the relationships among sexual and apomictic taxa; the nature of apomixis, whether obligate or facultative in individual plants, microspecies, and species; the constancy of the 4-nucleate unreduced embryo sacs in the subfamily; the genetics of apomixis including segregation of apomictic and sexual types in generations following crosses; further study of the interrelationships among apomixis, hybridization, and polyploidy; and the relationships between apomixis and geographical distribution at the specific, generic, and tribal levels.

Such studies could also result in some improved true-breeding forage varieties such as have come from the studies of apomixis in *Poa* by the

Carnegie Institution of Washington, Department of Plant Biology, under the direction of Dr. Jens Clausen at Stanford, California.

REFERENCES

- (1) BABCOCK, E. B., 1947. "The genus *Crepis*. I. The taxonomy, phylogeny, distribution, and evolution of *Crepis*." *University of California Press, Berkeley*.
- (2) BROWN, W. V. and W. H. P. EMERY, 1957a. "Some South African apomictic grasses." *Jour. So. Afric. Bot.* 23 : 123-125.
- (3) ——— 1957b. "Apomixis in the Gramineae, tribe Andropogoneae: *Themeda triandra* and *Bothriochloa ischaemum*." *Bot. Gaz.* 118 : 246-253.
- (4) ——— 1958. "Apomixis in the Gramineae: Panicoideae." *Amer. Jour. Bot.* 45 : (March)
- (5) BRYANT, G. D., 1952. "The apomictic mechanism in *Bouteloua curtipendula*." Unpublished Thesis, *University of Oklahoma, U.S.A.*
- (6) BURTON, G. W., 1948. "The method of reproduction in common Bahia grass, *Paspalum notatum*." *Jour. Amer. Soc. Agron.* 40 : 443-458.
- (7) CELARIER, R. P. and J. R. HARLAN., 1957. "Apomixis in *Bothriochloa*, *Dichanthium* and *Capillipedium*." *Phytomorph.* 7 : 93-102.
- (8) EMERY, W. H. P., 1957. "A study of reproduction in *Setaria macrostachya* and its relatives in the south western United States and northern Mexico." *Bull. Torr. Bot. Cl.* 84 : 106-121.
- (9) EMERY, W. H. P. and W. V. BROWN, 1958. "Apomixis in the Gramineae, tribe Andropogoneae: *Heteropogon contortus*." *Madrono* 14 : (June)
- (10) FARQUHARSON, L. I., 1955. "Apomixis and polyembryony in *Tripsacum dactyloides*." *Amer. Jour. Bot.* 42 : 737-743.
- (11) FISHER, W. D., E. C. BASHAW, and E. C. HOLT, 1954. "Evidence for apomixis in *Pennisetum ciliare* and *Cenchrus setigerus*." *Agron Jour.* 46 : 401-404.
- (12) GRUN, P., 1955. "Cytogenetic studies in *Poa*. III. Variation within *Poa nervosa*, an obligate apomict." *Amer. Jour. Bot.* 42 : 778-784.
- (13) GUSTAFSSON, A., 1946-1947. "Apomixis in higher plants, I, II, and III." *Lunds Univ. Arsskrift* 42 : 1-66, 43 : 71-178, 43 : 183-370.
- (14) HAIR, J. B., 1956. "Subsexual reproduction in *Agropyron*." *Heredity* 10 : 129-160.
- (15) HARTLEY, W., 1950. "The global distribution of tribes of the Gramineae in relation to historical and environmental factors." *Austral. Jour. Agric. Res.* 1 : 355-373.
- (16) HAYMAN, D. L., 1956. "Cytological evidence for apomixis in Australian *Paspalum dilatatum*." *Jour. Austral. Inst. Agric. Sci.* 22 : 292.
- (17) NARAYAN, K. N., 1951. "Apomixis in *Pennisetum*." Unpublished Thesis, *University of California, U.S.A.*
- (18) NARAYANASWAMI, S., 1954. "The structure and development of the caryopsis in some Indian millets. III. *Paspalum scrobiculatum* L." *Bull. Torr. Bot. Cl.* 81 : 288-299.
- (19) ——— 1955. "The structure and development of the caryopsis in some Indian millets. IV. *Echinochloa frumentacea* Link." *Phytomorph.* 5 : 161-171.
- (20) NYGREN, A., 1946. "The genesis of some Scandinavian species of *Calamagrostis*." *Hereditas* 32 : 131-262.

- (21) ——— 1954a. "Investigations on North American *Calamagrostis*." *Hereditas* 40 : 377-397.
- (22) ——— 1954b. "Apomixis in the Angiosperms. II." *Botan. Rev.* 20 : 577-649.
- (23) SNYDER, L. A., 1957. "Apomixis in *Paspalum secans*." *Amer. Jour. Bot.* 44 : 318-324.
- (24) SNYDER, L. A., A. R. HERNANDEZ, and H. E. WARMKE, 1955. "The mechanism of apomixis in *Pennisetum ciliare*." *Bot. Gaz.* 116 : 209-221.
- (25) STEBBINS, G. L. and E. B. BABCOCK, 1939. "The effect of polyploidy and apomixis on the evolution of species of *Crepis*." *Jour. Heredity* 30 : 519-530.
- (26) WARMKE, H. W., 1954. "Apomixis in *Panicum maximum*." *Amer. Jour. Bot.* 41 : 5-11.